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Original article

The elusive origin of *Chiosella timorensis* (Conodont Triassic)☆

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ABSTRACT

The First Appearance Datum (FAD) of the conodont *Chiosella timorensis* has been recently proposed as an index for the worldwide recognition of the Olenekian-Anisian Boundary (OAB, Early-Middle Triassic boundary). We here report the co-occurrence of *C. timorensis* with the ammonoids *Neopopanoceras haugi* (Hyatt and Smith), *Keyserlingites pacificus* (Hyatt and Smith), *Subhungarites yatesi* (Hyatt and Smith) and *Pseudacrochordiceras inyoense* (Smith), which are diagnostic of the late Spathian *Haugi* Zone. This shows that the previously published first occurrences of *C. timorensis* were still too poorly constrained, and it questions the adequacy of its FAD as a marker of the OAB. It challenges the significance of some observed lower stratigraphic occurrences of *C. gondolelloides* compared with *C. timorensis*. We revise the current criterion for the taxonomic separation of these two species and define a new *Chiosella* species (left in open nomenclature). The origin of *Chiosella timorensis* remains unknown but multi-element analyses suggest an affinity with the late Olenekian *Neogondolella* ex gr. *regalis*. Our reassessment of the material from the most important OAB sections (Desli Caira, Romania and Guandao, China) allows us to propose a new and more reliable biochronological scheme based on conodont maximal associations for the OAB.

1. Introduction

A platform morphology is frequently reduced/lost or, on the contrary, developed during the evolutionary course of pectiniform conodont elements. During the Early Triassic, progressive reduction of the platform is presumably exemplified by the *Neogondolella–Sweetospathodus–Neospathodus* lineage. Similarly, Nogami (1968) defined '*Gondolella*' *timorensis* as a '*Gondolella*' with a noticeably reduced platform. Kozur (1988), on the contrary (following Bender, 1968), erected the genus *Chiosella* on the assumption that forms like *Chiosella gondolelloides* and *C. timorensis* were transitional forms along a *Triassospathodus–Chiosella–Neogondolella* lineage, by which neospathodid (segminate) elements would have developed mid-lateral ridges and later gained platforms. This view is shared by most conodont workers, at least since the seventies (Bender, 1968) and it has historical grounds: at that time it was thought that elements like the P_1 of *Neogondolella* disappeared at the Permian-Triassic boundary (PTB) and re-evolved around the OAB through the proposed platform gain scenario. The type species of *Neogondolella* is a Middle Triassic species, so this naturally led Kozur (1988) to erect the pre-PTB genus *Clarkina*. More recently, however, it was shown that such elements were actually present throughout the Early Triassic (Orchard, 1994). Moreover, multi-element reconstructions demonstrated that some neogondolellid species of respectively late Permian, Smithian and early Anisian age shared this same apparatus (Orchard and Rieber, 1999). As the reconstructions by Orchard (2005) show, the ramiform elements were able to evolve quite rapidly too during the Early Triassic. So the fact that several species share the same apparatus tends to prove that they were pertaining to the same long-ranging taxon and the alternative view that their apparatuses are only homeomorphic, i.e. that they evolved several times independently, does not seem to be the most parsimonious scenario. Although it is largely contradicted by multi-element analysis, a polyphyletic origin for "*Neogondolella*" is similarly implied in a recent publication by Gradinaru et al. (2006), who redefined *C. timorensis* on the basis of the extension of its mid-lateral ridge. Indeed, Gradinaru et al. (2006) presented a newly reached consensus on a practical definition of *C. timorensis* relative to its presumed forerunner *C. gondolelloides*: authors formerly used different criteria to separate the two species and it was hoped that this would stabilize the taxonomy. In other occasions, this question could appear subsidiary, but it had been recognized that the first occurrence of *C. timorensis* appeared frequently very close to the Anisian base as defined by ammonoids (*Japonites welteri* beds; Bucher, 1989; see discussion). Its wide distribution (North America, Southern Europe, Pakistan, Japan, Timor, Australia) makes it particularly helpful for global correlations. Subsequently

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its First Appearance Datum (FAD) has been suggested as a potential index for a global definition of the Olenekian-Anisian Boundary (OAB, Early-Middle Triassic boundary).

The confusion concerning the recognition of *C. timorensis* arose in part because it is impossible to distinguish between juveniles of *C. timorensis* and juveniles or even adult specimens of *C. gondolelloides*. Orchard (1995) noted that adult specimens of both *Chiosella* species are usually distinguished by their relative length and the relative width of the rudimentary platform. Yet, the "*Neospathodus*" *timorensis* illustrated by Sweet (1970) is a demonstrative example of the difficulties herewith involved: in all the above mentioned aspects (relative length of the element and relative width of the rudimentary platform) it appears identical to both Nogami's (1968) holotype and Gradinaru et al.'s figured specimen of *C. timorensis* (pl. 1, figs. 1, 2 figs. 1, 2 in Gradinaru et al., 2006); it is nevertheless regarded as an (upper Spathian?) "advanced" form of *C. gondolelloides*. In fact the difference lies in the posterior extension of the median ridge which, according to the new definition (Gradinaru et al., 2006; see also Kozur, 1988; Bachmann and Kozur, 2004), "reaches the posterior denticle of the unit at least on one side [...] of the blade". This particular morphology is observed more commonly in Anisian strata, but as shown here, the criterion is no longer tenable as a defining feature of Anisian morphotypes.

2. Geological settings

The present study is based on the analysis of a representative rock sample collected by one of us (J.J.) from his JJ7-07 locality, south of John Brown Canyon, in the Northern Humboldt Range, Nevada (N40° 29′ 8.8", W118° 07′ 38.2"; see Fig. 1). This locality is believed to correspond to the M2834 locality from which Norm Silberling reported *Haugi* Zone ammonoids (Silberling and Wallace, 1969). Medium-gray to dark, thin-bedded micritic limestones of the carbonate unit of the lower Member of the Prida Formation are poorly exposed on this slope and the presently studied sample corresponds to a representative sampling of matrix from several float blocks found in close proximity, each of which contained *Haugi* Zone ammonoids. The ammonoid fauna is composed of: *Neopopanoceras haugi* (Hyatt and Smith, 1905), *Keyserlingites pacificus* (Hyatt and Smith), *Subhungarites yatesi* (Hyatt and Smith) and *Pseudacrochordiceras inyoense* Smith. "*Acrochordiceras*" *inyoense* has been reassigned by Tozer (1994) to the new genus *Pseudacrochordiceras*, which clearly differs from the exclusively Anisian *Paracrochordiceras*. This association is diagnostic of the upper part of the late Spathian *Haugi* Zone (Bucher, 1989; Guex et al., 2010). It is found at the top of the carbonate unit of the lower Member of the Prida Formation (Star Peak Group), i.e. some 20 to 30 m stratigraphically below the base of the Anisian (Fossil Hill Member, *Japonites welteri* beds). It is separated from the *J. welteri* beds by the Brown Calcareous Sandstone, which is a lateral equivalent of the deltaic Dixie Valley Formation, which crops out in the eastern part of the basin (Bucher, 1992). It records the worldwide regression straddling the Lower-Middle Triassic boundary (Embry, 1997).

3. Material and methods

About 3 kg of rocks were dissolved in buffered acetic acid (Jeppsson et al., 1999). The residues were then treated for concentration by density separation using Sodium-Polytungstate (Jeppsson and Anehus, 1999). Several independent runs were processed, which invariably yielded the same results in terms of conodont faunal content: namely the presence of *Triassospathodus homeri*, *Neogondolella* ex. gr. *regalis*, and *Chiosella timorensis*.

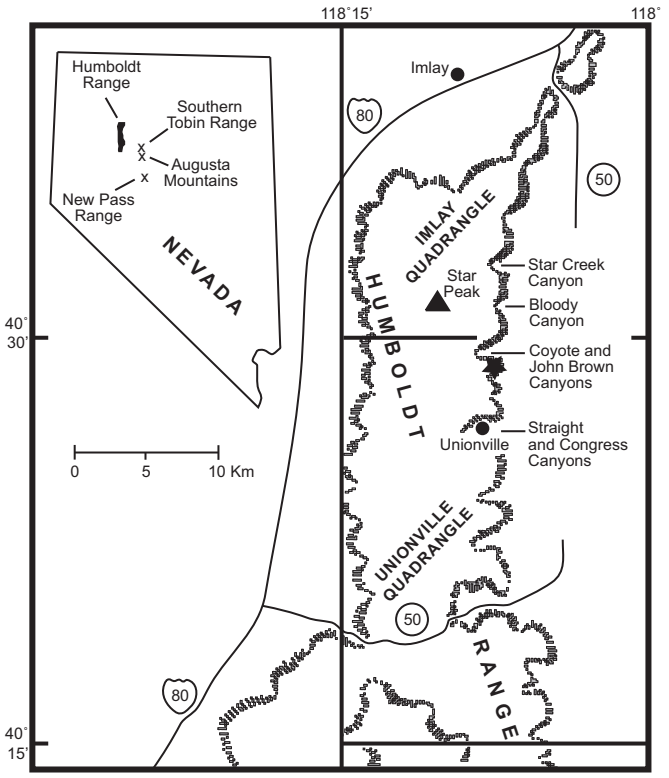

Fig. 1. Geographical setting. The mentioned JJ7-07 locality is indicated by a star.

Indeed, as illustrated on Figs. 2 and 3, some *Chiosella* specimens do exhibit the distinctive "*timorensis*" posterior extension of the midlateral ridge, and, following the criterion suggested by Gradinaru et al. (2006), are therefore referred to *C. timorensis*. Furthermore, as explained below we no longer assign elements like *C. timorensis* (for a description of what this 'like' includes, see next section) that lack the posterior extension of the midlateral ridge to *C. gondolelloides*, but include them in *C. timorensis*. *C. gondolelloides* is also redefined and a new *Chiosella* species is described.

The preservation of the present material is moderate and the colour of the elements is dark brown.

4. Systematic palaeontology (N.G. and M.J.O.)

Figured specimens are housed with the Paleontological Institute and Museum of the University of Zurich (numbers designated below by PIMUZ), Karl Schmid-Strasse 4, 8006 Zurich, Switzerland.

Suprageneric classification mostly follows Donoghue et al. (2008).

Class CONODONTA Eichenberg, 1930
Division PRIONIODONTIDA Dzik, 1976
Order OZARKODINIDA Dzik, 1976
Superfamily GONDOLELLOIDEA (Lindström, 1970)
Family GONDOLELLIDAE Lindström, 1970
Subfamily NEOGONDOLELLINAE Hirsch, 1994
Currently revised by Goudemand et al. (ongoing work).
Genus **Chiosella** Kozur, 1989

Type species and holotype: *Gondolella timorensis* Nogami, 1968 (pp. 127–128, pl. 10, fig. 17a–c).

Type stratum and locality: Lacan, Manatuto county, Timor.

Diagnosis (Kozur, 1988: pp. 415–416): Based on segminate to segminiplanate P1 elements with a very narrow or rudimentary

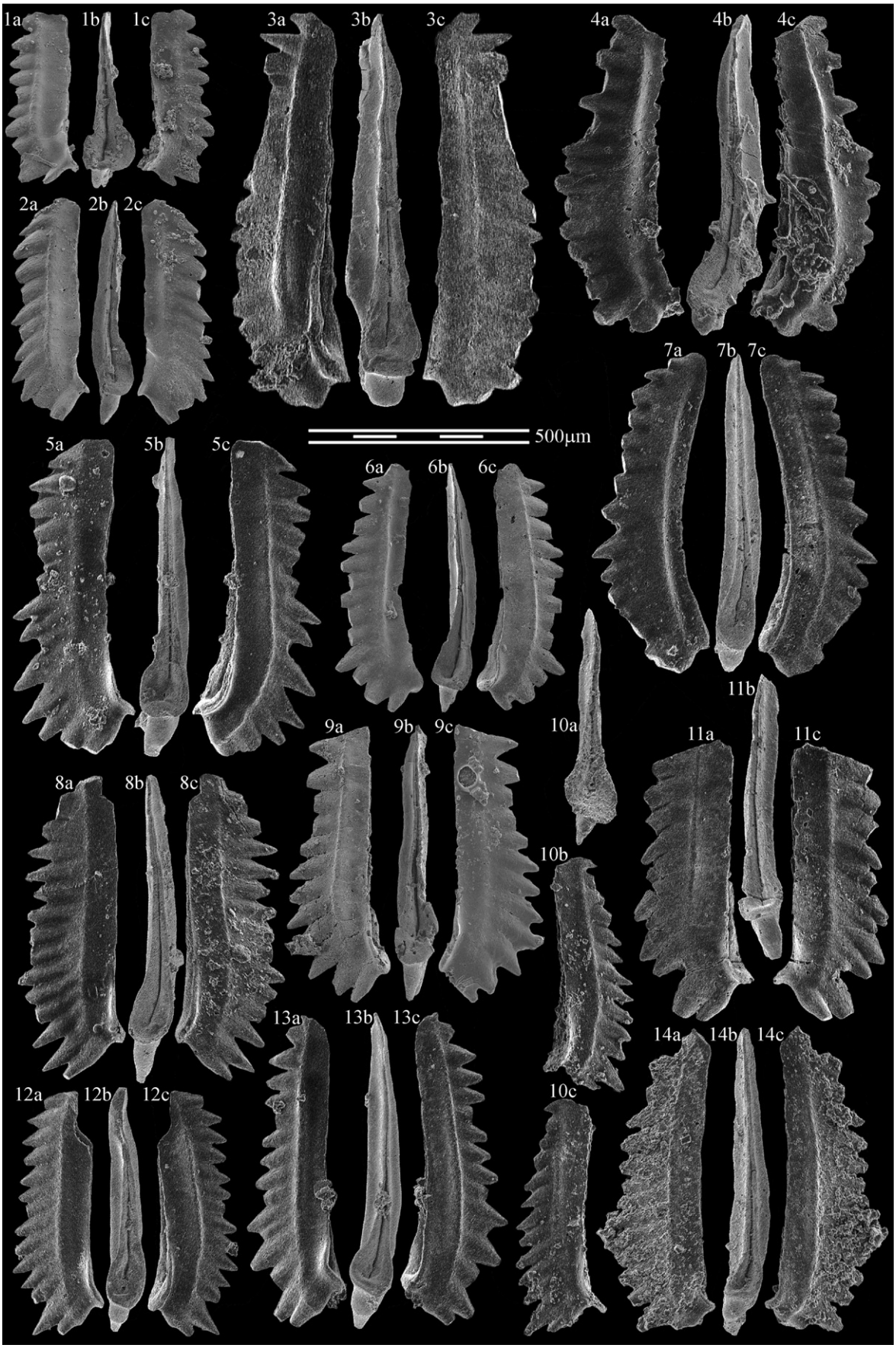

Fig. 2. 1–14. *Chiosella timorensis*, PIMUZ 28738-28751. Aboral and lateral views. All specimens from sample JJ7-07, Nevada. Spathian.

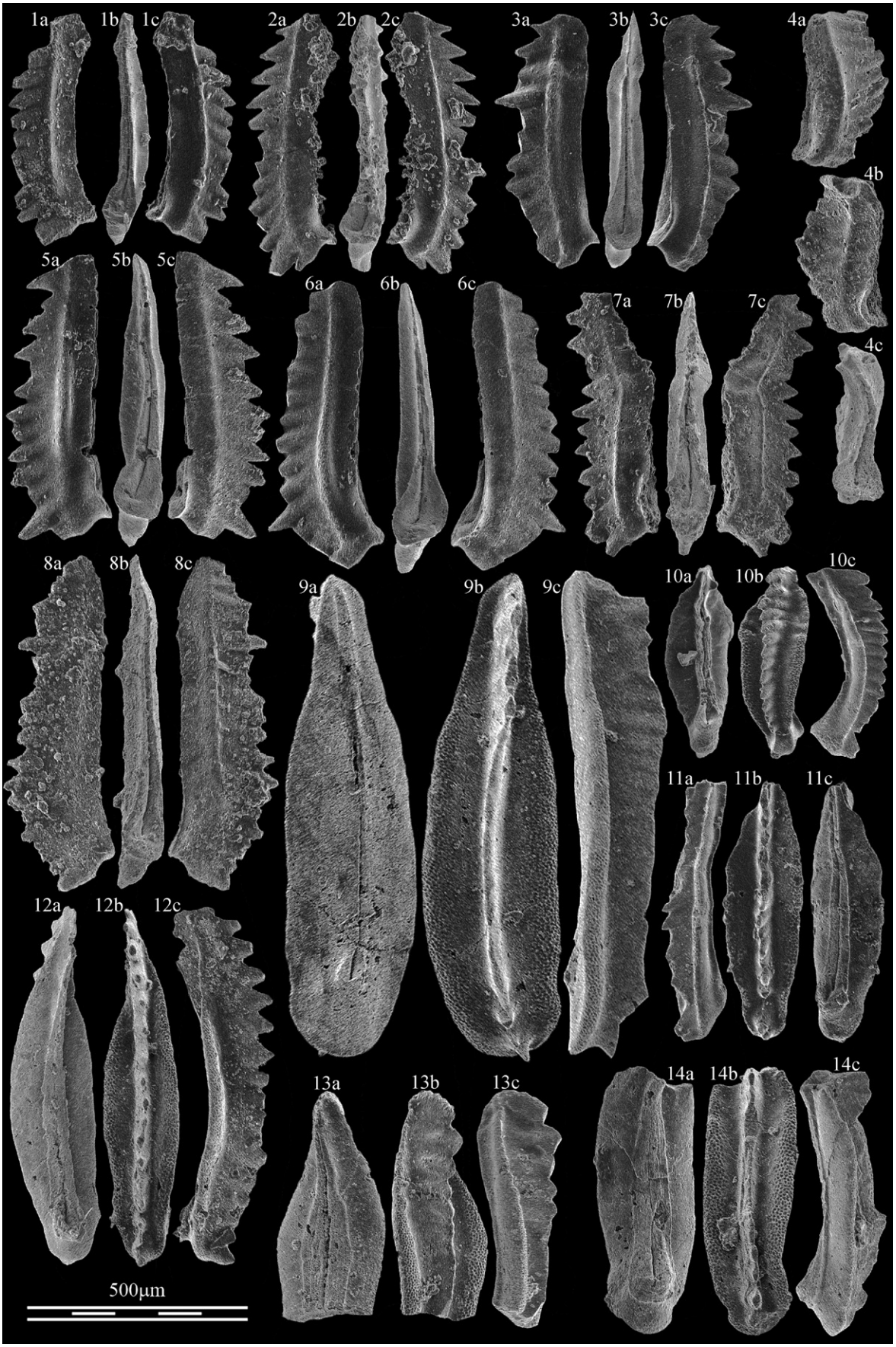

Fig. 3. 1–8. *Chiosella timorensis*, PIMUZ 28752-28759. Aboral and lateral views. **9, 11–14**. *Neogondolella* ex. gr. *regalis*, PIMUZ 28760, 28762-28765. Aboral, oral and lateral views. **10**. *Neogondolella* n. sp. A, PIMUZ 28761. Aboral, oral and lateral views. All specimens from sample JJ7-07, Nevada. Spathian.

platform developed, commonly asymmetrically, on each side of a high carina.

Multi-element diagnosis (Orchard, 2005): As for *Neogondolella*, except for the characteristic P1 element.

Chiosella? gondolelloides (Bender).

1968. *Chiosella*? *gondolelloides* Bender - Pl. 5, fig. 17; re-illustrated in Orchard, 1995, figs. 2.4, 2.5.

Diagnosis (Orchard, 1995): Species distinguished by relatively elongate segminate elements with a blade that in later growth stages bears a low longitudinal ridge along most of its length. The denticles are moderately fused and increasingly reclined to the posterior, where a larger, posteriorly projecting denticle is located. The lower margin of the basal cavity is elliptical in outline and is expanded beneath the posterior one-third to one-half of the element.

Remarks: The holotype was re-illustrated and described by Orchard (1995). It is partly broken and its preservation does not allow unambiguous determination of similar elements. It was for instance compared with, and said to be similar to "*Neospathodus*" *symmetricus*, except that the latter would lack a conspicuous lateral rib. However, in the type collection of '*N*'. *symmetricus* from Oman a few specimens apparently do have a lateral rib. The latter is faint and not really conspicuous but the same applies to the holotype of *C. gondolelloides*. Its denticulation appears to be different but again the fact that most of the holotype's denticles are broken is not particularly helpful. For these reasons we consider that this species may include only its holotype. Previously this species included also elements that were in all aspects similar to *C. timorensis* but lacked the posterior extension of the midlateral rib. These are now included in *C. timorensis*. It included also relatively shorter and higher elements that we now assign to *C.* n. sp. B.

Chiosella timorensis (Nogami).

Figs. 2(1–14), 3(1–8).

1968. *Gondolella timorensis* Nogami, pp. 127–128, pl. 10, figs. 17–21.

1970. *Neogondolella aegea* Bender, p. 516, pl. 3, figs. 21–26(29).

1970. *Spathognathodus gondolelloides* Bender, pp. 529-530, pl. 5, figs. 19, 20.

1970. *Neospathodus timorensis* - Sweet, p. 256, pl. 2, figs. 22, 23.

1977. *Neogondolella timorensis* - Nicora, pp. 92–98, pl. 1–4, all figs. except fig. 3 of pl. 3.

1992. *Gondolella timorensis* - Gaetani et al., p. 195, pl. 17, figs. 8–13.

1994. *Chiosella timorensis* - Orchard, pl. 1, figs. 1–10, 12–14.

2006. *Chiosella timorensis* - Gradinaru et al., pl. 1, figs. 1–7.

2007a. *Chiosella timorensis* - Orchard et al., figs. 5(32–34).

2007b. *Chiosella timorensis* - Orchard et al., figs. 6(32–34, 36–38).

Diagnosis: See diagnosis of the genus.

Remarks: Available specimens correspond to the thorough description given by Sweet (1970), except that a secondary posterior process bearing one or two denticles is not necessarily present. At all stages of growth, the cusp may or may not be terminal (note that elements with a big terminal cusp are excluded from the present definition: they have been differentiated already by Orchard; see *Chiosella* n. sp. A sensu Orchard et al., 2007a, 2007b). The downward deflection of the posterior end varies also more than suggested by Sweet: in most specimens the basal margin is straight or substraight for most of the unit's length and deflected downwardly posterior of the cusp, but in some specimens (e.g., Fig. 2(7)) the basal margin is curved along the whole length of the element and no distinctive deflection can be observed posterior of the cusp. These forms may deserve differentiation in the future but for now they are retained within the present taxa. This species is also rather variable in general profile, development of lateral ribs (that extend or not to the posterior-most denticle), shape, number and extent of fusion of denticles. Yet, we consider that some forms with distinctively smaller length: height ratio should be separated (see *Chiosella*? n. sp. B). We illustrate also two presumably teratological or pathological specimens of *C.* cf. *timorensis* on Fig. 3(4,7).

Chiosella n. sp. B.

2005. *Chiosella*? sp. A, Orchard, text-fig. 12, part A.

2006. *Chiosella gondolelloides* - Gradinaru et al., pl. 1, figs. 8–12.

2007a. *Chiosella gondolelloides* - Orchard et al., fig. 5, parts 13–15, 23–25.

2007b. *Chiosella gondolelloides* - Orchard et al., fig. 6, parts 25–29.

Description: Segminate elements with moderate length: height ratio (2.5–2.7:1), about 9 to 12 relatively broad denticles that are gradually more reclined to the posterior, and whose free tips are subequilaterally triangular in shape. The height is maximal on the third or fourth denticle from the posterior end and decreases slowly in both directions from there. The cusp is the broadest denticle. One or two smaller denticles stand behind the cusp, the terminal one being conspicuously less broad than the adjacent ones.

Remarks: Compared with *C. timorensis*, which it most closely resembles, this species is relatively shorter and higher and it has less numerous and broader denticles of distinctive triangular shape.

Genus **Neogondolella** Bender and Stoppel, 1965

1989. *Clarkina* Kozur, pp. 428–429.

Type species and holotype: *Gondolella mombergensis* Tatge, 1956 (p. 132, pl. 6, fig. 2a–c).

Type stratum and locality: Upper Muschelkalk, Schmidtdiel Quarry, Momberg, near Marburg.

Original diagnosis: Segminiplanate P1 elements with strong, partly fused carina of variable height ending in a (sub)terminal cusp. These elements were previously included in *Gondolella* Stauffer and Plummer.

Multi-element diagnosis: As described by Orchard (2005) and Orchard and Rieber (1999), except that the dolobrate element is now considered to be in the S1 position and the S2 position is occupied by the 'enantiognathiform' breviform digyrate element (Goudemand et al., ongoing work). A thorough discussion can be found in Orchard and Rieber (1999).

Neogondolella ex. gr. *regalis* Mosher.

Fig. 3(9, 11–14).

1970. *Neogondolella regale* Mosher, pp. 741–742, pl. 10, figs. 1, 4.

Diagnosis (Mosher, 1970): P1 elements of *Ng. regale* have a platform extending the full length of the unit and a prominent carina of mostly fused, nearly subequal denticles.

Remarks: Mosher (1970) included Spathian forms within the range of this species. Nicora (1977) noted however that older specimens (from the *Subrobustus* Zone) differ substantially by having a large, flat platform and a lower carina, and should be referred to another species. This was also the opinion of Orchard (1994) who considered that these forms are only superficially similar to the type species. Hence their assignment to *Ng.* ex gr. *regalis*, pending revision of the neogondolellids of this interval. The herein illustrated specimens strongly resemble *Neogondolella* elements illustrated by Orchard et al. (2007a, 2007b) and occurring around the OAB at Guandao and Desli Caira, respectively. They also closely resemble much older (early Spathian) *Neogondolella* elements that occur in our collections from Darwin Canyon, California.

Neogondolella n. sp. A.

Fig. 3(10).

Description: This (juvenile) element has a platform, which is broadest at about one-third of the unit from the anterior end and tapers gradually at both ends. Anteriorly, the platform is conspicuously serrated and the corresponding carinal denticles are laterally expanded in a manner that recalls those of *Icriospathodus collinsoni*. The terminal cusp is very big and markedly separated from the moderately high denticles of the anterior process. In lateral view the unit is strongly arched.

Remarks: This species is based on a single specimen. Hence it is kept in open nomenclature.

5. Discussion

The above mentioned co-occurrence of *C. timorensis* (sensu Gradinaru et al., 2006) with ammonoids classically regarded as late Spathian questions both the nature of *C. timorensis* as a presumed index for the O-A boundary and its presumed higher stratigraphic first occurrence compared with *C. gondolelloides*, which until now lend some support to the platform gain scenario.

5.1. Previous observations

Many authors discussed the age of *C. timorensis* and some of them (e.g., Mirauta in Atudorei et al., 1997) already considered that the first occurrence of this species was below the OAB (then implicitly defined on ammonoids). Based on a re-assessment of many OAB boundary collections, Gradinaru and co-workers (2006) concluded that, based on their new definition of the species, the first occurrence of *C. timorensis* is Anisian and is in fact a good index for the OAB. In this respect our new observations are quite surprising.

Wang Z. (1982) also described the occurrence in Ziyun (South China) of *C. timorensis* in strata where Wang Y.G. (1978, 1984) had already found an unusual assemblage of Spathian and Anisian ammonoids. Unfortunately the reported bed from Ziyun is in fact a synsedimentary slope breccia (H.B., pers. observation) comprising a mixture of essentially late Spathian ammonoids associated with a few early Anisian ones.

According to Nogami (1968), the holotype of *C. timorensis* (from his sample 041 collected near Ue Lacan in Timor) could have been either latest Scythian (Spathian) or Anisian in age. The identifications of the associated ammonoids (*Leiophyllites timorensis* Bando and *Procarnites* aff. *kokeni* (Arthaber)) are problematic. If correctly identified, *Procarnites* would indicate a Spathian age, exclusively. The age significance of this material was also addressed by Nicora (1977: pp. 96–97). However, the co-occurrence of *C. timorensis* together with *Gl. tethydis* in his sample suggests that the holotype is in fact Anisian in age (see below) and that the original identifications of the associated ammonoids are inconsistent.

Until now, the best argument (Kozur, 1988; Orchard, 1995) for the separation of both *Chiosella* species using the current criterion (Gradinaru et al., 2006) is the apparent earlier occurrence of *C. gondolelloides* in several sections over the world, notably at the Desli Caira section in Romania, where the OAB can also be placed using the ammonoid faunal succession (Orchard et al., 2007a). The First Occurrence (FO) of *C. gondolelloides* is about 3 m below the proposed OAB (sample 9038), whereas the FO of *C. timorensis* was observed to be in sample GR7 (before reassessment, see below), which contains also the oldest Anisian ammonoids of the section. However, we advise caution in interpreting the completeness of this record because of the nature of the condensed Hallstatt-type limestones, the abrupt excursion of the carbon stable isotope curve (Atudorei in Atudorei et al., 1997; Atudorei, 1999), and the apparent absence of several ammonoid maximal association zones known elsewhere (compare with Bucher, 1989 and Guex et al., 2010).

According to Gradinaru et al. (2006: p. 35), in the Pietra dei Saracini section (Sicily) and in several sections in Turkey, the relative locations of both FOs are similar to those in the Desli Caira section, but no published data is yet available for those sections.

At the type locality of *C. gondolelloides* in Marathovuno on Chios island, Greece (section CM II, Bender, 1968), if we trust the occurrence table (p. 488; vs. captions, see below), the FO of *C. gondolelloides* (8.5 m) is about two meters below that of '*Neogondolella*' *aegea* (10.5 m; this name is now considered a junior synonym of *C. timorensis*; see Nicora, 1977 and Gradinaru et al., 2006). Note also that the (erroneous?) caption of two illustrated specimens of '*Neogondolella*' *aegea* (pl. III, figs. 21, 22; caption p. 537; '*Neogondolella*' *timorensis benderi* Nicora) indicates an occurrence three meters (5.5 m level) below the FO of *C. gondolelloides*. Furthermore, a later report by Assereto et al. (1980), who re-examined Bender's localities, outlined problems of fissure fillings and erosion channels. They mentioned more especially the considered interval (CMII, 8.5-10 m), for which their conodont faunas differ completely from those of Bender (1980: p. 730, last paragraph). They could not confirm a lower occurrence of *C. gondolelloides* (CMII, 8.5 m) and suggested that the corresponding report by Bender might be due to erroneous sampling. At the much more expanded Guandao section in South China, the FOs of both species are almost synchronous (same bed in Upper Guandao, only 10 cm difference in Lower Guandao; Orchard et al., 2007b). Unfortunately, as for the Chios section, no ammonoid data is available that would provide an independent age control. If the respective Chinese FOs are in the *Welteri* Zone then we may expect (if additional sampling were available) a lower FO of *C. gondolelloides* in the Chinese section (as assumed by Orchard et al., 2007b). Alternatively, if they are in the *Haugi* Zone as we show to be the case in Nevada, we will rather expect a lower FO of *C. timorensis* in Romania (if we assume that both FOs have similar relative positions globally, but of course the FO of one or both species can be diachronous on a global scale).

5.2. Reassessment of the material: rare specimens

At the Lower Guandao section, China, the first *Chiosella* occurrences are relatively rare (*Triassospathodus homeri* still predominates in the fauna). Furthermore, and in absence of any clear facies change, several beds of this densely sampled section where *Chiosella* is apparently absent (a dozen samples corresponding to 1-2 m at the Lower Guandao section) separate these first occurrences from the interval where *Chiosella* eventually predominates. This even led Orchard et al. (2007b) to suggest that the OAB (defined as the FAD of *C. timorensis*) could actually be located up to three meters below the base of Upper Guandao samples (OU numbers) within a less densely sampled interval. In lower Guandao, among the first and rare *Chiosella*, pectiniform elements assigned to *C. timorensis* represent less than 4% (2 specimens over about 60) of all *Chiosella* pectiniform elements.

At Desli Caira, a similar distribution of those taxa in the lowest *Chiosella*-bearing rocks may explain the apparent absence of *C. timorensis* in those beds. In fact, a close re-examination of the Romanian material revealed that one specimen in sample 9038 (Orchard et al., 2007a: fig. 3), formerly identified as *C. gondolelloides*, exhibits faint posterior extension of the midlateral rib. As in some Nevadan specimens, in lateral view a conspicuous bump of the posterior edge of the cusp or posteriormost denticle is clearly visible. The same observation applies to a specimen from sample OU2 (Orchard et al., 2007b: fig. 5) from the upper Guandao section, immediately below the appearance of more characteristic *C. timorensis*. This emphasizes the difficulty of consistently applying the former species criteria in smaller collections. In the Nevadan collection, the number of specimens available is much higher,

which enhanced the chance of finding at least some specimens that have a more conspicuous and hence more easily identifiable rib posteriorly.

5.3. Reliability of the platform gain scenario

How reliable is then the evidence that the FO of *C. gondolelloides* is older than that of *C. timorensis*? And if they are contemporaneous, how are they related to each other? Could the observed distribution of both taxa alternatively reflect intraspecific variation (*C. timorensis* as big, robust variant of *C. gondolelloides*) and/or ontogenetic trajectory (*C. timorensis* as adult, or gerontic form of *C. gondolelloides*)? We know that *Neogondolella* was already present prior to the appearance of *Chiosella*, so the similarity of their respective apparatuses supports the notion that the origination of *Chiosella* is from *Neogondolella* rather than from *Triassospathodus*, i.e. through platform loss in P_1 elements rather than through platform gain (Orchard, 2005: p. 87). If this were the case, the presumed precursor (*C. gondolelloides*) of *C. timorensis* is unlikely to have less prominent platforms/ribs.

Let us take another example of presumed platform loss in the course of Early Triassic evolution, namely the case of *Sweetospathodus kummeli*. '*Neospathodus*' *kummeli* was introduced by Sweet (1970) to designate a species whose P_1 elements are comblike, twice as long as high; with up to 16 subequal denticles; a straight or downwardly convex basal margin; and a prominent midlateral rib. Its generic reassignment to *Sweetospathodus* by Kozur et al. (1998) reflects the widely accepted idea that P_1 elements like this should have evolved from neogondolellid (platform-bearing, segminiplanate) forms, presumably from *Neogondolella*, and are transitional to neospathodid (*Neospathodus*-like, i.e. short segminate) forms. Sweet (1970: p. 251) noted that the midlateral rib "varies greatly in prominence from one specimen to another" and "may be produced laterally into a platform-like brim in specimens representing intermediate and late growth stages".

We consider that within known *Chiosella* populations the extension of the platform is probably an intraspecific variable character that bears no clear stratigraphic information. Separation of both taxa should rather be based on other criteria. Some relatively short and high forms previously included in *C. gondolelloides* are absent from our Nevadan collection, and these deserve separation from *C. timorensis*. Due to the poor preservation of Bender's holotype, their assignment to a new species is here favoured (*Chiosella*? n. sp. B, see previous section).

5.4. Reassessment of the material: new Tethyan conodont biozonation at the OAB

Using our new definitions (see previous section), we reassessed the collections of the two currently best OAB sequences (Desli Caira and Guandao). The corresponding new occurrence tables are found in Fig. 4; highlighted are the proposed association zones. The color coding enables easy recognition and shows how these zones or rather 'beds' are correlated from one place to the other.

The (blue) '*triangularis* beds' are defined by the local occurrence of '*Neospathodus*' *triangularis*. In our Chinese collections this species is usually restricted to the mid-upper Spathian *Prohungarites* beds (see also Orchard, 1995). Its occurrence very close below the FO of *Chiosella* spp. suggests that it partly extends into the *Haugi* Zone in this region. A single element occurs in bed G7B at Desli Caira and it may well be an example of reworking. Nevertheless, in the Salt Range (Pakistan) Sweet (1970) reported the co-occurrence (in samples K1-50 and T63-167) of this species with *Chiosella timorensis*. Hence this informal biozone may be only local and not laterally reproducible.

The (yellow) '*carinata* beds' are characterized by the co-occurrence of *Gladigondolella carinata* with either *Chiosella timorensis* or *Chiosella* n. sp. B. They correlate with the late Spathian *Haugi* Zone (upper part) and the *Stevensi* Zone (latest Spathian; Guex et al., 2010). It is not clear yet whether *Gl. carinata* extends into the (classically Anisian) *Welteri* Zone.

The (red) '*tethydis* beds' are characterized by the co-occurrence of *Gladigondolella tethydis* with either *Triassospathodus homeri* or *Spathicuspus spathi*. Based on the illustrations of the poster presented by Gradinaru and Sobolev at the Boreal Triassic 2006 conference (associated abstract without illustrations: Gradinaru and Sobolev, 2006), the upper part of these '*tethydis* beds' in Desli Caira (ammonoid beds 204/821) would record the occurrence of typically Anisian ammonoids (pl. 2, fig. 4 is an involute japonitid ammonoid). It is not clear what ammonoids occur in the lower part (beds G7c, d) of these "*tethydis* beds" in Desli Caira. The precise stratigraphical location of the ammonoids reported by Gradinaru and Sobolev (2006) around this interval is not provided. Their specimen of *Karangatites* sp. is reinterpreted here as *Eodanubites* sp. (a late Spathian genus). Their *Paracrochordiceras* sp. is an acrochordiceratid (possibly a *Paracrochordiceras* sp.) of Anisian affinity. Hence these '*tethydis* beds' have a rather Anisian affinity, but a better documentation of the ammonoids (including a precise occurrence table with associated plates) is needed in order to be conclusive.

Further work is necessary in order to assess the lateral reproducibility of these biozones. Hence, they are provisionally called 'beds' rather than given the formal status of zones. As far as the conodonts are concerned, the OAB should preferably be located between the "*carinata*" and the "*tethydis* beds". Note that in the Lower Guandao section, the local maximal horizon corresponding to the "*carinata* beds" is sample O40, where *Gl. carinata* is also associated with *Ch.* n. sp. A. This association is still uncertain in Desli Caira but if it is confirmed there and in other sections in the future, it may enable to add another association zone and to refine the biochronological scheme within this critical time interval.

Based on the above definition, the OAB remains bracketed by the two ash layers PGD-2 and PGD-3 at Lower Guandao section (Lehrmann et al., 2006, 2007) and the previous 247.2 Ma age estimate of the Early-Middle Triassic boundary given by Lehrmann et al. (2007) still holds. Adjustment in the boundary position yields a new slightly younger age estimate comprised between 247.16 Ma and 247.17 Ma, these two values corresponding respectively to the lower and upper bounds of the uncertainty interval within which the OAB should be located.

5.5. Origin of Chiosella

As discussed above, an evolutionary lineage leading from *C. timorensis* to *Ng.* ex gr. *regalis* was first described by Bender and Kockel (1963) and Bender (1968), and reiterated by others (Nicora, 1977: p. 98; Gradinaru et al., 2006); it actually led to the establishment of *Neogondolella* (Orchard and Rieber, 1999). However, *Ng.* ex gr. *regalis* forms occur much lower than *Chiosella* in the Spathian (Orchard, 1994), which contradicts the derivation of the former from *C. timorensis*. If the presumed phylogenetic relationship holds, as also reflected by their similar apparatuses, it should be interpreted as directed in the opposite way, i.e. *Chiosella timorensis* should derive from *Neogondolella* ex gr. *regalis*. Furthermore, we observe that the earliest *Chiosella* representatives appear comparatively longer and lower than later representatives (including *C.* n. sp. A sensu Orchard et al., 2007a, 2007b or *C.* n. sp. B (this work)), and early juveniles of *C. timorensis* (for instance in sample OU3 of the Upper Guandao section) most closely resemble subcontemporaneous juveniles of *Neogondolella*, except that they miss the platform of the latter. This again is an argument in favour of the platform loss scenario contra an origin in *Triassospathodus*.

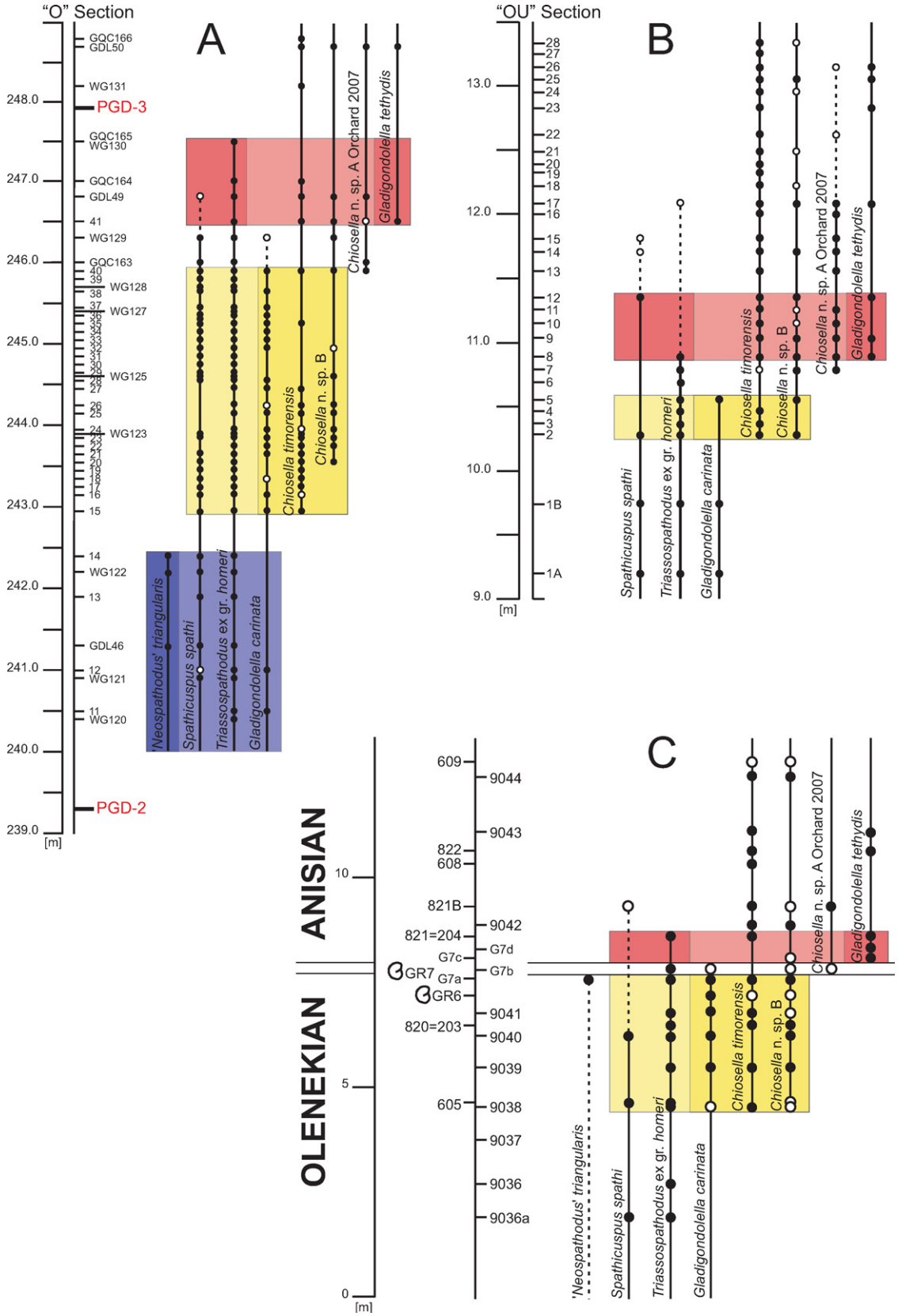

Fig. 4. Revised distribution of conodont taxa around the OAB at both Guandao sections **(A, B)** and at the Desli Caira section **(C)** (modified after Orchard et al., 2007a, 2007b). Full circle: confirmed occurrence; open circle: questionable occurrence. Note that the scale of the Lower Guandao section has been corrected to be congruent with data from Lehrmann et al. (2007). See the online electronic version of this paper for references to colours in the text.

Yet, pending taxonomic revision of the neogondolellids of this time interval including *Ng.* ex gr. *regalis*, the origin of *C. timorensis* remains unclear.

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